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Neural correlates of perceptual grouping effects in the processing of sound omission by musicians and nonmusicians.

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Title: Neural correlates of perceptual grouping effects in the processing of sound omission by musicians and nonmusicians

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Abstract: Perceptual grouping is the process of organizing sounds into perceptually meaningful elements. Psychological studies have found that tones presented as a regular frequency or temporal pattern are grouped according to gestalt principles, such as similarity, proximity, and good continuity. Predictive coding theory suggests that this process helps create an internal model for the prediction of sounds in a tone sequence and that an omission-related brain response reflects the violation of this prediction. However, it remains unclear which brain areas are related to this process, especially in paying attention to the stimuli. To clarify this uncertainty, the present study investigated the neural correlates of perceptual grouping effects. Using magnetoencephalography (MEG), we recorded the evoked response fields (ERFs) of amateur musicians and nonmusicians to sound omissions in tone sequences with a regular or random pattern of three different frequencies during an omission detection task. Omissions in the regular sequences were detected faster and evoked greater activity in the left Heschl's gyrus (HG), right postcentral gyrus, and bilateral superior temporal gyrus (STG) than did omissions in the irregular sequences. Additionally, an interaction between musical experience and regularity was found in the left HG/STG. Tone-evoked responses did not show this difference, indicating that the expertise effect did not reflect the superior tone processing acquired by amateur musicians due to musical training. These results suggest that perceptual grouping based on repetition of a pattern of frequencies affects the processing of omissions in tone sequences and induces more activation of the bilateral auditory cortex by violating internal models. The interaction in the left HG/STG may suggest different styles of processing for musicians and nonmusicians, although this difference was not reflected at the behavioral level.

*Highlights (for review)
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Highlights:

- Sound omission in a tone sequence elicits the omission-related response (OR).
- We studied the effect of perceptual grouping on ORs.
- ORs were measured in musicians and nonmusicians using magnetoencephalography.
- ORs were increased by perceptual grouping and localized in the auditory cortex.
- The grouping effect was left-side dominant in musicians but not in nonmusicians.

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Neural correlates of perceptual grouping effects in the processing of sound omission by musicians and nonmusicians

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Keywords:

Perceptual grouping, Omission, Predictive coding theory, Magnetoencephalography, Musical experience

Abbreviations:

OR, omission-related response; MEG, magnetoencephalography; HG, Heschl's gyrus; STG, superior temporal gyrus; MMN, mismatch negativity; ISI, inter-stimulus interval; AC, auditory cortex; MRI, magnetic resonance imaging; RMS, root mean square; ANOVA, analysis of variance; RT, reaction time; SD, standard deviation.

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Abstract

Perceptual grouping is the process of organizing sounds into perceptually meaningful elements. Psychological studies have found that tones presented as a regular frequency or temporal pattern are grouped according to gestalt principles, such as similarity, proximity, and good continuity. Predictive coding theory suggests that this process helps create an internal model for the prediction of sounds in a tone sequence and that an omission-related brain response reflects the violation of this prediction. However, it remains unclear which brain areas are related to this process, especially in paying attention to the stimuli. To clarify this uncertainty, the present study investigated the neural correlates of perceptual grouping effects. Using magnetoencephalography (MEG), we recorded the evoked response fields (ERFs) of amateur musicians and nonmusicians to sound omissions in tone sequences with a regular or random pattern of three different frequencies during an omission detection task. Omissions in the regular sequences were detected faster and evoked greater activity in the left Heschl's gyrus (HG), right postcentral gyrus, and bilateral superior temporal gyrus (STG) than did omissions in the irregular sequences. Additionally, an interaction between musical experience and regularity was found in the left HG/STG. Tone-evoked responses did not show this difference, indicating that the expertise effect did not reflect the superior tone

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processing acquired by amateur musicians due to musical training. These results suggest that perceptual grouping based on repetition of a pattern of frequencies affects the processing of omissions in tone sequences and induces more activation of the bilateral auditory cortex by violating internal models. The interaction in the left HG/STG may suggest different styles of processing for musicians and nonmusicians, although this difference was not reflected at the behavioral level.

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1. Introduction

In an orchestral performance, a musical piece is produced by multiple sequences of tones played in parallel. The auditory system can extract the structural components of the piece, such as its melody and rhythm, from this mixture of tones using processes that integrate acoustic information over time. Together, these processes are called perceptual grouping, and psychological studies have identified the rules for grouping sound features, such as similarity, proximity or good continuity (Bregman, 1990; Deutsch, 2012; Koffka, 1935). Bregman (1990) suggested that two types of perceptual grouping exist: one is stimulus-driven and works preattentively in a short time window, while the other requires higher cognitive functions such as attention and/or experience-based knowledge, and has a longer time window.

A wording to predictive coding theory, cortical circuits create internal models to generate predictions about incoming stimuli (Friston and Kiebel, 2009a, 2009b; Friston, 2005). An evoked response may occur reflecting the transient expression of a prediction error, which results from comparison between the bottom-up inputs from lower cortical/subcortical areas and top-down predictions from higher cortical areas. Several studies have applied this theory to explain the early stages of auditory processing (Bendixen et al., 2012; Winkler and Czigler, 2012; Winkler, 2007; Winkler et

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al., 2009). Key to this explanation is that an internal model is created by spectral or temporal regularity, which is extracted from a tone sequence. Mismatch negativity (MMN) and the omission-related response (OR), both of which are elicited by deviation (a deviant tone or the omission of a tone) from a sequence of repetitive tone stimuli, can be interpreted as resulting from the violation of the prediction. In particular, the OR is suitable for investigating prediction-related brain activity because it does not overlap with the response elicited by the stimulus. Previous studies have shown that an OR can be elicited by a tone omission in an unattended tone sequence at an inter-stimulus interval (ISI) of less than 200 ms (Alain et al., 1989; Hughes et al., 2001; Raij et al., 1997; Snyder and Large, 2005; Tarkka and Stokic, 1998; Todorovic et al., 2011; Wacongne et al., 2011; Yabe et al., 2001, 1997). Together with Bregman's idea and the predictive coding theory, these results can be interpreted as resulting from a violation of a prediction based on pre-attentive perceptual grouping based on temporal regularity. The OR in the absence of attention is localized in the auditory cortex (AC) (Raij et al., 1997; Todorovic et al., 2011), which may be involved in prediction and pre-attentive perceptual grouping.

Several neurophysiological studies have elicited ORs at an ISI longer than 200 ms when the participants paid attention to the stimuli (Alain et al., 1989;

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Joutsiniemi and Hari, 1989; Penney, 2004). These results suggest that an OR to tone sequences with long ISI can occur as a result of a violation of a prediction based on attentive perceptual grouping. However, the neural correlates of this phenomenon remain unclear. Thus, we aimed to find the neural correlates of prediction based on attentive perceptual grouping in a tone sequence with a regular frequency pattern. We hypothesized that, when participants paid attention to the stimuli, a repetitive frequency pattern would cause perceptual grouping and help create stronger predictions about incoming stimuli, compared to a tone sequence with a random pitch pattern. Thus, a violation of this prediction by an omission in a tone sequence with a pitch pattern would evoke a stronger OR than would an omission in a random tone sequence. To clarify this issue, we compared the brain magnetic responses evoked by omissions in regular and random tone sequences using magnetoencephalography (MEG).

In addition, we evaluated the impact of musical experience on the grouping effect. Musical training normally includes the structural analysis of musical pieces, which should improve the ability to extract regular patterns from a tone sequence because the structural components of a piece (e.g., melody, chord progression, meter, etc.) are established by pitch and/or rhythm patterns. Although psychological studies have demonstrated that perceptual grouping depends on experience (Bhatara et al.,

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2013; Dewar et al., 1977; Gobet and Simon, 1996; Idson and Massaro, 1976; Iversen et al., 2008; Saariluoma, 1989; Simon and Chase, 1973), no study has investigated the neural correlates of this phenomenon. Thus, we tested the hypothesis that musical training influences the brain mechanisms involved in the perceptual grouping of frequency patterns, leading to more pronounced patterns of cortical activation in musicians than in nonmusicians.

2. Methods

2.1 Participants

The participants consisted of 13 amateur musicians (7 males and 6 females) who regularly played musical instruments, such as piano, guitar, violin, and cello, with an average experience of 13 ± 5 years (mean ± standard deviation [SD]), and 14 nonmusicians (11 males and 3 females) who had no instrumental experience, except for lessons in school. All participants were right-handed with an average age of 22 ± 2 years and provided written informed consent to participate in the experiment. Although we did not measure the participants' hearing thresholds, none of them reported difficulty in discriminating the stimuli. The participants also did not report any neurological or

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hearing problems. The experiment was performed in accordance with the ethical standards of the Declaration of Helsinki and the guidelines approved by the local ethics committee of the Graduate School of Medicine and Faculty of Medicine, Kyoto University.

2.2 Stimuli

Pure tones (50-ms duration, 5-ms onset/offset ramps, 65 dB SPL) with three different frequencies (C5: 523 Hz, E5: 659 Hz, and G5: 784 Hz) were created as wave files using the Audacity software program (ver. 2.0.3; http://audacity.sourceforge.net/). A silent period with a length of 500 ms was created as the omission stimulus. Each tone sequence was constructed of these tones, presented either in a regular pattern of “CEG” (regular sequence) or pseudo-randomly (irregular sequence), with an ISI of 450 ms (Fig. 1A). In the irregular sequence, randomization was controlled so as not to present the same frequency more than three times consecutively, and at least three tones were presented between omissions.

2.3 Procedure

Participants were seated in a chair in a magnetically shielded room. The tone sequences

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were presented through earphones, which was coupled to the ear by a silicon tube and the ear insert (E-A-R-tone 3A, Aearo Corporation, Indianapolis, USA). The earphone was connected to an amplifier (Roland SRQ-2031, Roland Corporation, Hamamatsu, Japan) outside of the shielded room. Participants were instructed to press a button with their right index finger as quickly as possible upon noticing any omission in the sequence. Because perceptual grouping facilitates the processing of deviant stimuli in a tone sequence (Idson and Massaro, 1976; Jones et al., 1982; Mondor and Terrio, 1998; Royer and Garner, 1970), the response time was used to characterize the effect of perceptual grouping.

Each sequence was presented in three separate blocks. Six blocks were conducted in total, and the order of the blocks was randomized between participants. In each block, approximately 7% of the tones were replaced with a silent period. In total, 2520 tones and 180 omissions (60 omissions for each tone) were presented in regular and irregular sequences. An additional restriction for the regular sequence was that, after each omission, the sequence started again from the C tone (e.g., CEGCEGCE_CEG…) to maintain the repetition of the CEG pattern.

At the end of the experiment, we asked the participants whether they had recognized the regular sequence as a CEG pattern, and all participants reported that they

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had.

2.4 MEG acquisition

Event-related fields (ERFs) were recorded with a 306-channel whole-head magnetoencephalography (MEG) system (Vectorview, Elekta Neuromag Oy, Finland). The head position was determined using four indicator coils attached to the scalp. In addition, three head landmarks (the nasion and bilateral preauricular points) and head shape were recorded for each participant using a spatial digitizer (Polhemus Inc., Colchester, VT, USA) before the experiment. These data were used for co-registration with the T1 anatomical image of each participant obtained using a 0.2 T magnetic resonance imaging (MRI) machine (Signa Profile, GE Health Care, Waukesha, WS, USA). The ERFs were recorded with a band-pass filter (0.1 to 200.0 Hz) and a sampling rate of 600 Hz. To reduce external noise, we used spatiotemporal signal space separation (tSSS) methods (MaxFilter, Elekta Neuromag Oy, Helsinki, Finland) with a correlation window of 900 s, which covered the entire length of each block, and a correlation limit of 0.980. The acquired data were low-pass filtered using a fifth-order Butterworth zero-phase filter with a cut-off frequency of 40 Hz. The time window of each epoch lasted between 50 ms prestimulus and 450 ms poststimulus, and the prestimulus period

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was used for baseline correction. Peak-to-peak differences of more than 3.0 pT/cm were used as rejection criteria.

2.5 MEG sensor level analysis

To analyze the temporal waveform of the brain response evoked by omission at the sensor level, we calculated the root mean square (RMS) values of 20 planar gradiometers that separately covered the temporal lobe in the right and left hemispheres. The same array of sensors was employed in all participants. Because the observed waveforms of the brain response evoked by omission exhibited a gradual increase with no specific peak, the mean value from 100 to 400 ms after omission onset was analyzed using four-way analysis of variance (ANOVA) with the factors musical experience, regularity, position of omission (C, E, or G tone), and laterality (left or right hemisphere) using R software (ver. 2.15.2; R Foundation for Statistical Computing, Vienna, Austria; http://www.R-project.org). Post-hoc analyses were conducted using lower-level ANOVAs and paired *t*-tests with multiple comparison using Shaffer’s modified Bonferroni correction (Shaffer, 1986).

2.6 MEG source level analysis

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To localize the possible source of the OR and compare the activation of the source between conditions, we used an empirical Bayesian approach, as implemented in SPM8 (Welcome Trust Centre for Neuroimaging, University College London, UK). Participants' T1 images were normalized to the Montreal Neurological Institute (MNI) brain template, and the inverses of the parameters were used to wrap a cortical template mesh to each individual MR space. Co-registration between the MEG sensor positions and T1 images was achieved by manually detecting three fiducial points in both the MR image and the head-shape measurement taken using the spatial digitizer. To generate the forward model, the lead-field for each sensor was calculated for the dipoles at each point in the cortical mesh using a single shell model. The model was then inverted using the multiple sparse priors (MSP) algorithm (Friston et al., 2008; Mattout et al., 2006). To evaluate the cortical distribution evoked by omission in detail, reconstructed maps were created for each 100-ms time window from 100 to 400 ms after omission onset. These maps were exported as three-dimensional images into the MNI space and smoothed using a Gaussian filter with a 12-mm full-width at half maximum (FWHM).

For group analysis, general-linear-model-based statistical analysis with random field theory was conducted using SPM8. To visualize the averaged distribution of brain activation evoked by omission, the reconstructed maps for the omission of C, E, and G

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tones between 100 and 400 ms after omission onset were pooled separately for the regular and irregular sequences and analyzed by one-sample *t*-tests, comparing the activation with zero, at an uncorrected threshold of $p < 0.005$. To investigate the effects of the experimental variables, we conducted a three-way ANOVA with the factors musical experience, regularity, and position of omission at an uncorrected threshold of $p < 0.001$ for each 100 ms window from 100 to 400 ms after omission onset. All maps were projected to the MNI template. The MNI coordinates of these voxels were then converted to Talairach space using GingerALE (Laird et al., 2010), and Talairach Client was used for anatomical labeling (Lancaster et al., 2007). To further investigate the time course of the contribution of activated areas, we conducted region of interest (ROI) analysis. The amplitude of each dipole in a 10-mm diameter circle centered upon the selected ROI in the cortical mesh was averaged for each time point for each participant. The mean of these values at each 100-ms time window from 100 to 400 ms was then calculated. The ROI activity was then analyzed using ANOVAs.

To test the possibility that the effect of musical experience on the OR simply reflected the larger brain response elicited by tones in musicians, as shown in previous studies (Pantev et al., 2003, 1998), we conducted a source level analysis for tone-evoked ERFs. Reconstructed maps were created in the same way as for the OR and

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analyzed using a three-way ANOVA with the factors musical experience, regularity, and position of omission.

2.7 Behavioral data analysis

The time difference between the onset of omission (the time at which the missing tone had been expected) and the button press was calculated as reaction time (RT). The mean and SD of the RT were analyzed using a three-way ANOVA with the factors musical experience, regularity, and position of omission. Post-hoc analyses were conducted using lower-level ANOVAs and paired *t*-tests with multiple comparisons using Shaffer's modified Bonferroni correction (Shaffer, 1986).

3. Results

3.1 Behavioral data

The group mean RT is presented in Fig. 1B. A three-way ANOVA with the factors musical experience, regularity, and position of omission showed main effects of regularity (F [1, 25] = 5.24, p = 0.031) and position of omission (F [2, 50] = 6.68, p = 0.002), although neither a main effect nor an interaction related to musical experience

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were observed. Multiple comparisons revealed that the omission of the C tone was detected faster than omissions of the other tones. The three-way ANOVA of the SD also showed main effects of regularity (F [1, 25] = 7.71, p = 0.010) and position of omission (F [2, 50] = 6.54, p = 0.003). Multiple comparisons revealed that the SD for the omission of the C tone was larger than omissions of the other tones. The rate of correct detection for the omissions was over 95%, and did not vary significantly across conditions.

(Fig. 1 around here)

3.2 Analysis of magnetic fields evoked by omissions

An example of the ERF waveform for one musician (Fig. 1C) is typical in not showing a clear peak; instead, the amplitude increased gradually after 100 ms of omission onset. The group means of the RMS values of the responses evoked by the omissions are plotted in Fig. 2. A four-way ANOVA with the factors musical experience, regularity, position of omission, and laterality showed main effects of regularity (F [1, 25] = 30.04, p < 0.001) and laterality (F [1, 25] = 6.27, p = 0.019), although no main effect or interaction related to musical experience were observed. These results indicate that

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omission evoked a larger brain response for regular than for irregular sequences, irrespective of musical experience (Fig. 3).

(Fig. 2 and Fig. 3 around here)

Fig. 4A depicts the average cortical activation between 100 and 400 ms after omission onset. Despite the lack of stimulus input, activation was observed in the bilateral temporal and frontal lobes. Three-way ANOVAs with the factors musical experience, regularity, and position of omission for each 100 ms time window from 100 to 400 ms after omission onset showed similar results. From 100 to 200 ms, the analysis showed a main effect of regularity in the left Heschl's gyrus (HG) and right postcentral gyrus, as well as an interaction between musical experience and regularity in the left HG. From 200 to 300 ms, the ANOVA showed a main effect of regularity in the bilateral superior temporal gyrus (STG) and an interaction between musical experience and regularity in the left STG. These areas showed stronger activation in response to omission in regular than in irregular sequences (Fig. 4B). From 100 to 200 ms and 200 to 300 ms, an interaction between musical experience and regularity was found in the left STG (Fig. 4C). No main effects or interactions were detected from 300 to 400 ms.

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The peak coordinates of the activated areas are listed in Table 1.

(Fig. 4 and Table 1 around here)

To further analyze the interaction between musical experience and regularity in the left STG from 100 to 300 ms, we conducted a ROI analysis for this area. The mean ROI activity was analyzed using separate two-way ANOVAs with the factors musical experience and time (100 to 200 ms, 200 to 300 ms) for the regular and irregular sequences. For the regular sequences, the ANOVA showed main effects of musical experience (F [1, 25] = 5.91, p = 0.023) and time (F [1, 25] = 19.05, p < 0.001), indicating stronger activation in musicians than in nonmusicians (Fig. 5). The ANOVA for the irregular sequences showed no significant differences.

(Fig. 5 around here)

To test the possibility that the differences in the activated areas observed between musicians and nonmusicians were based on differences in the brain activation evoked by tones, the cortical distribution of the activation was analyzed using a

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three-way ANOVA with the factors musical experience, regularity, and position of omission. No significant difference in activation was observed for each 100 ms time window from 100 to 400 ms after tone onset, indicating that musical training did not yield greater cortical activation by the pure tones employed in the present experiment.

4. Discussion

Both behavioral and neurophysiological differences were observed in the processing of omissions between regular and irregular sequences. Better detection performance and larger ERFs were associated with omissions in regular sequences than in irregular sequences. Source-level analysis showed that omissions in the regular sequences elicited stronger activation in the bilateral HG/STG than did those in the irregular sequences. Based on predictive coding theory, these results can be interpreted to indicate that activity in the auditory cortex is related to the matching between an internal predictive model and an actual stimulus input.

4.1 Influence of perceptual grouping on the processing of sound omission

We expected that the repetition of C, E, and G tones in a fixed order (CEGCEG…)

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would elicit perceptual grouping of the pitch pattern (CEG). The participants' faster detection performance for the regular sequence agrees with the results of previous studies, which have shown that perceptual grouping improves the detection and recognition of target stimuli (Idson and Massaro, 1976; Jones et al., 1982; Mondor and Terrio, 1998; Royer and Garner, 1970). In addition, the participants reported recognizing the regular sequence as a repetition of a CEG pattern. Therefore, we believe that the fixed order presentation of the C, E, and G tones in the regular sequence elicited perceptual grouping of the CEG pattern.

From a predictive coding perspective, our results can be interpreted as follows: the perceptual grouping of the CEG pattern strengthened top-down modulation from higher-level brain areas and allowed stronger predictions to be created about incoming tones than for the irregular sequences. Disagreement between this prediction and the input caused a larger prediction error in the regular sequence, resulting in a larger OR. This was reflected by the significant activation difference around the bilateral HG/STG between the regular and irregular sequences, suggesting that these regions were engaged in comparing the prediction with the stimulus input. The meaning of the activation in the right postcentral gyrus is, however, unclear. To the best of our knowledge, no previous study has examined the involvement of this region in perceptual grouping.

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Future research may clarify the importance of the region for this process.

Predictive coding theory based interpretation of the OR has previously been applied to results of experiments in which the participants were instructed to ignore the stimuli (Bendixen et al., 2012, 2009; Winkler and Czigler, 2012; Winkler, 2007; Winkler et al., 2009). For example, Bendixen et al. (2009) used repetition of a pair of tones with 150-ms ISI and found that the amplitude of the OR depended on the predictability of the tones. This predictability-dependent difference was observed within 100 ms after omission onset, suggesting the occurrence of stimulus-driven prediction. Our findings can also be interpreted in light of this theory: in the present case, the prediction was created by modulation from a higher cortical level, such as attentional modulation. The latency difference of the OR between Bendixen et al (2009) and the present study may reflect this difference in type of prediction. This explanation would be in line with that of Bregman (1990), who suggested two mechanisms for perceptual grouping, a rapid stimulus-driven mechanism and a slower mechanism based on higher cognitive functions such as voluntary attention and/or experience-based knowledge. In light of the predictive coding theory and Bregman’s theory, the results of Bendixen et al (2009) may reflect stimulus-driven prediction and pre-attentive perceptual grouping, while our findings may reflect top-down prediction and attentive perceptual grouping.

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4.2 Impact of musical experience on perceptual grouping

For omission in the regular sequence, musicians showed stronger activation in the left STG than did nonmusicians, suggesting a stronger contribution of the left auditory cortex in perceptual grouping. This result is in line with those of previous studies, which have shown that the left hemisphere contributes to musical processing in musicians during behavioral tasks (Bever and Chiarello, 1974; Burton et al., 1989; Messerli et al., 1995) and neuroimaging studies (Boh et al., 2011; Evers et al., 1999; Hirshkowitz et al., 1978; Matsui et al., 2013; Ono et al., 2011; Vuust et al., 2005). Left-hemisphere dominance in analytical listening and right-hemisphere dominance in holistic listening have been proposed, as has the idea that musicians' left hemisphere contribution to auditory processing reflects an analytical listening strategy that differs from the holistic listening strategy of nonmusicians (Bever and Chiarello, 1974; Burton et al., 1989; Johnson, 1977; Messerli et al., 1995; Morais et al., 1982; Peretz and Morais, 1983). Musical training generally includes the structural analysis of musical phrases as well as practice with musical instruments. This training may induce analytical listening of tone sequences, which may be reflected by the stronger activation in the left STG in musicians than in nonmusicians.

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While brain activity showed expertise effects, behavioral performance did not show such effects. Although the reason for this incongruity is unclear, task demand may be involved. Because the rate of correct detection was over 95 %, the task may have been too easy for both musicians and nonmusicians, resulting in a ceiling effect. In this case, it would have been difficult to find significant differences between the groups. A more complicated task requiring more cognitive resources may have led to a significant difference between musicians and nonmusicians at the behavioral level. Additionally, the difference of listening strategy between musicians and nonmusicians may not have led to differing performance in the detection task. Finally, the fact that all musicians were amateurs may have contributed to the incongruity of the behavioral and MEG data. Although we did not question the participants regarding the length of their musical training per day or week, they were not trained as intensively as professional musicians. This degree of musical training may have been insufficient to result in a behavioral difference.

Another measure for which we did not find an effect of musical experience was the tone-evoked response. This result is not surprising as the effects of musical experience appear in a use-dependent manner (Lütkenhöner et al., 2006; Pantev et al., 2001, 1998). For example, Pantev et al. (1998) found an increase in the N1 response to

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piano tones in musicians that did not occur for pure tones. While piano tones are often encountered in musical training, pure tones are rarely experienced. Thus, after long-term musical training, more neurons may be involved in processing musical stimuli, while no change may occur for the brain processing of pure tones.

5. Conclusions

In summary, the perceptual grouping of pitch pattern in a tone sequence affected the processing of omissions in the sequence, both behaviorally and neurophysiologically. Our findings are in general agreement with those of earlier work suggesting the predictive nature of the auditory system. In addition, our results suggest that perceptual grouping elicited higher predictability for tones in a regular sequence, allowing for the faster detection of omissions, and also engaged the bilateral HG/STG in comparing the prediction and stimulus. Musical experience also influenced the neural processing of omissions, possibly reflecting a difference in listening strategy acquired through long-term musical training.

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Legends

Fig. 1

Sequence of stimuli and behavioral performance in the detection task. **A.** Sequence of stimuli used in the experiment. In the regular sequence, C, E, and G tones were presented as a repetition of a CEG pattern, whereas in the irregular sequence the tones were presented pseudo-randomly. **B.** Reaction time in the detection task. Error bars display the standard error of the mean (SEM). M = musicians; NM = nonmusicians. **C.** Examples of the magnetoencephalography (MEG) waveform evoked by the omission of the C tone in the irregular sequence for one musician. Waveforms from 20 gradiometers that covered the temporal lobe in each hemisphere were superimposed.

Fig. 2

Time course of the root mean square (RMS) amplitude of the omission-related response (OR). **A.** RMS amplitude of the OR in musicians. **B.** RMS amplitude of the omission-related response in nonmusicians.

Fig. 3

RMS amplitude of the brain response evoked by the omission between 100 and 400 ms

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after omission onset. The asterisks represent $p < 0.001$.

Fig. 4

Reconstructed maps showing significantly activated brain areas and the results of the three-way analysis of variance (ANOVA) with the factors musical experience, regularity, and position of omission. **A.** Visualization of the brain areas significantly activated between 100 and 400 ms after sound omission in the regular and irregular sequences, as determined by one-sample *t* tests (uncorrected $p < 0.005$). **B.** Brain areas showing a main effect of regularity in the three-way ANOVA for the time windows from 100 to 200 ms and from 200 to 300 ms (uncorrected $p < 0.001$). **C.** Brain areas showing an interaction between musical experience and regularity in the three-way ANOVA for the time windows from 100 to 200 ms and from 200 to 300 ms (uncorrected $p < 0.001$). L = left; R = right.

Fig. 5

Mean amplitude of the region of interest (ROI) activity. The ROI was located in the left superior temporal gyrus (STG), which was defined by the brain area showing the interaction between musical experience and regularity in the three-way ANOVA for the

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time windows from 100 to 200 ms and from 200 to 300 ms (Fig. 4C). M = musicians; NM = nonmusicians. A.U. = arbitrary unit.

Figure 01
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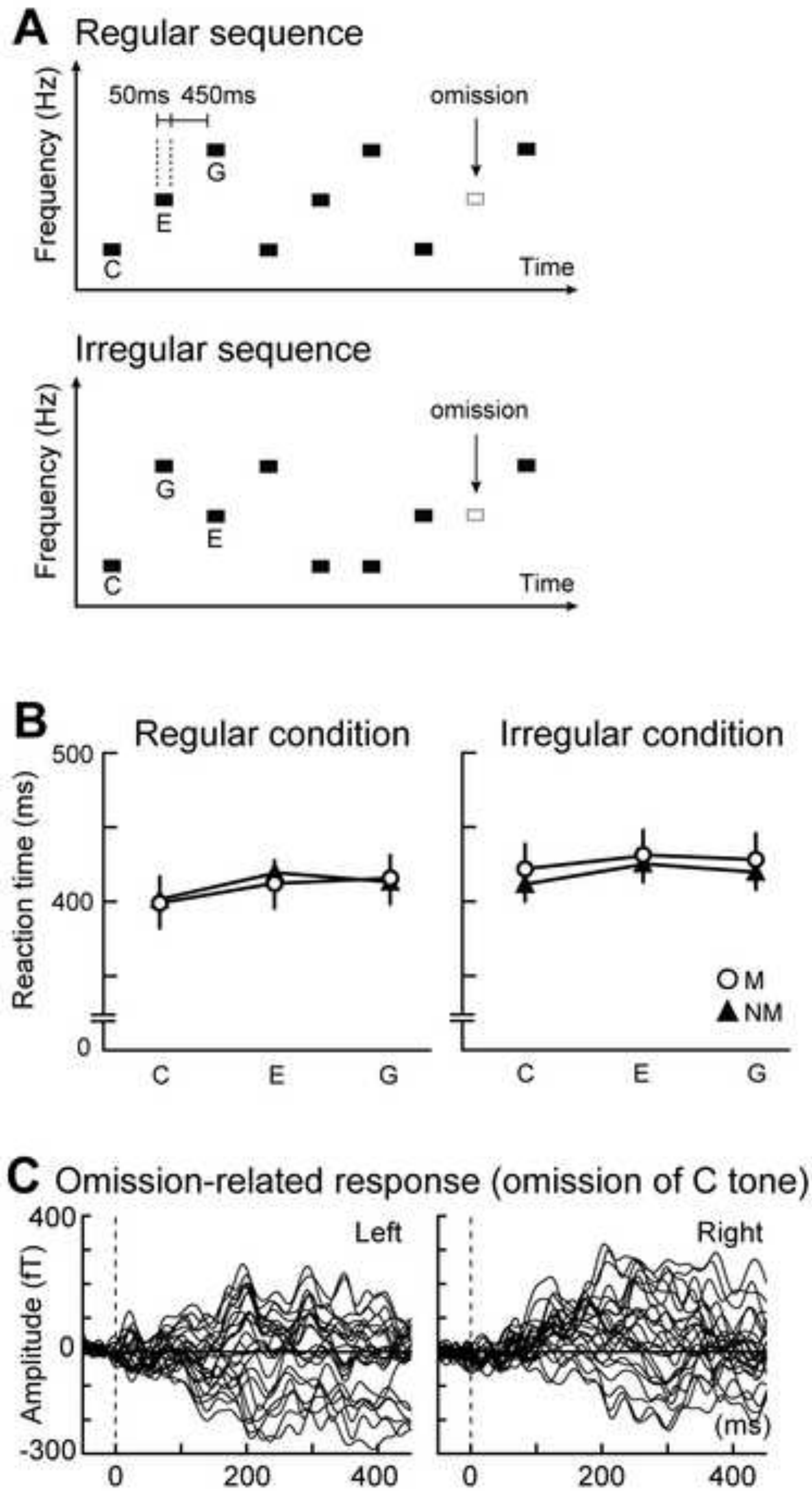

Figure02

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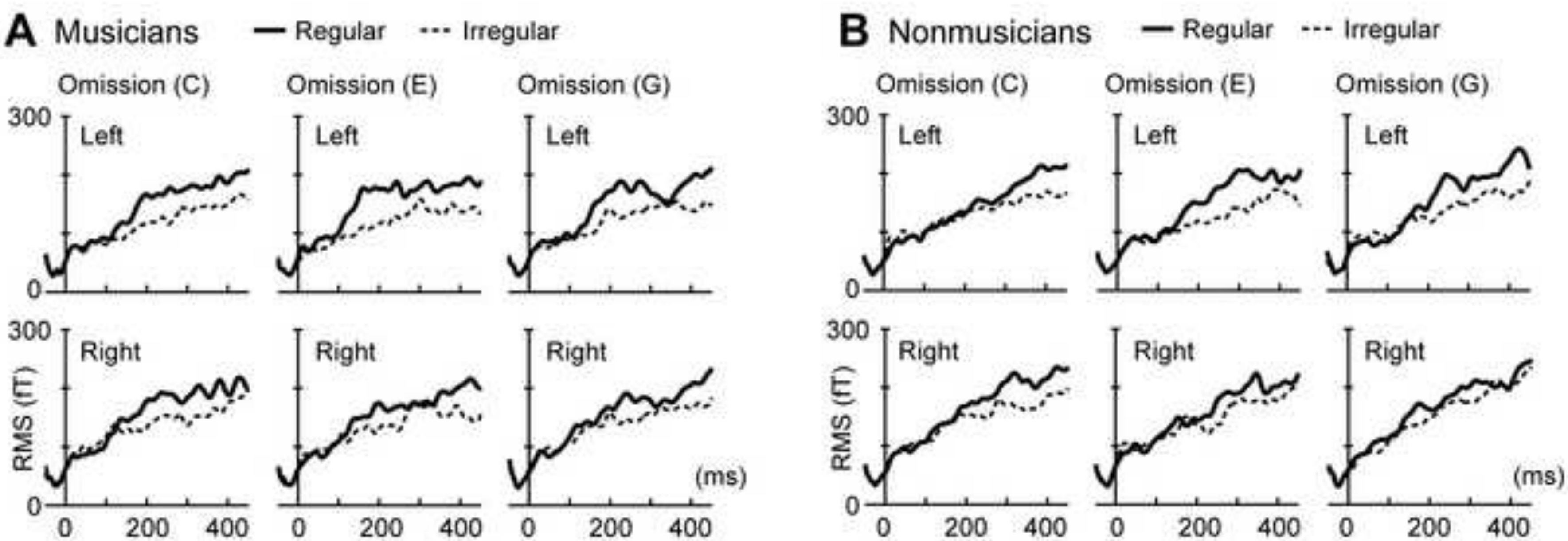

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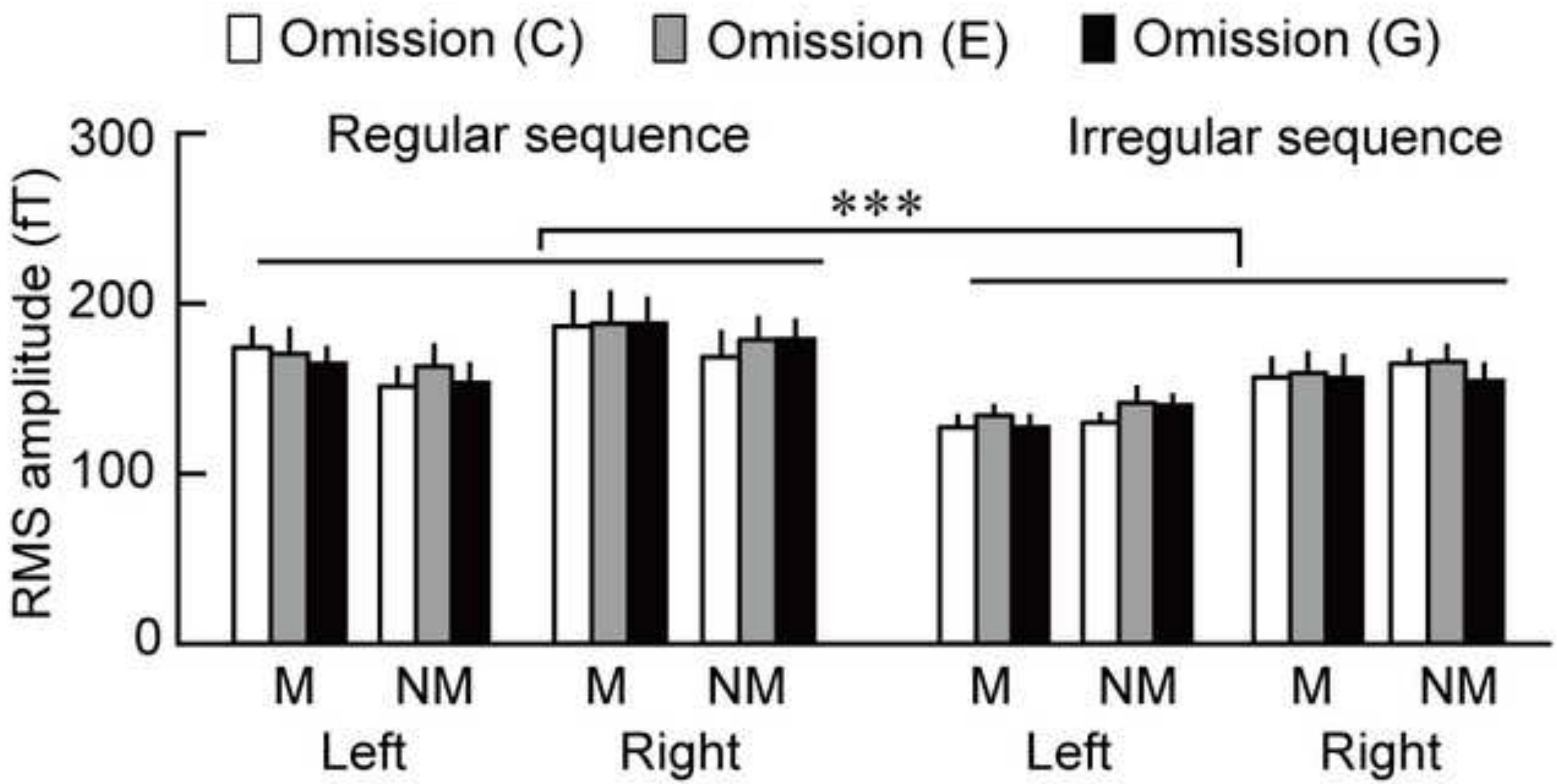

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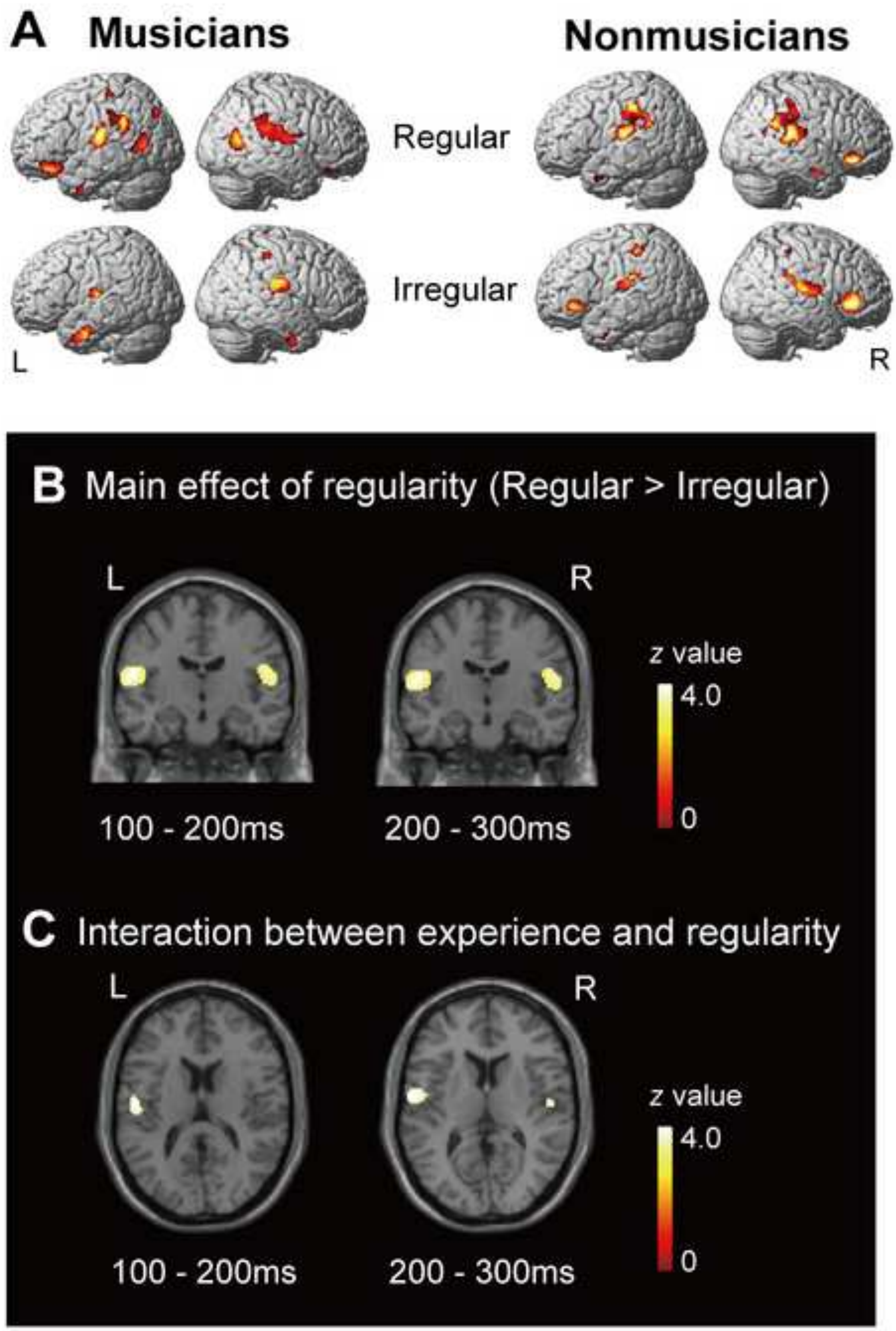

Figure05
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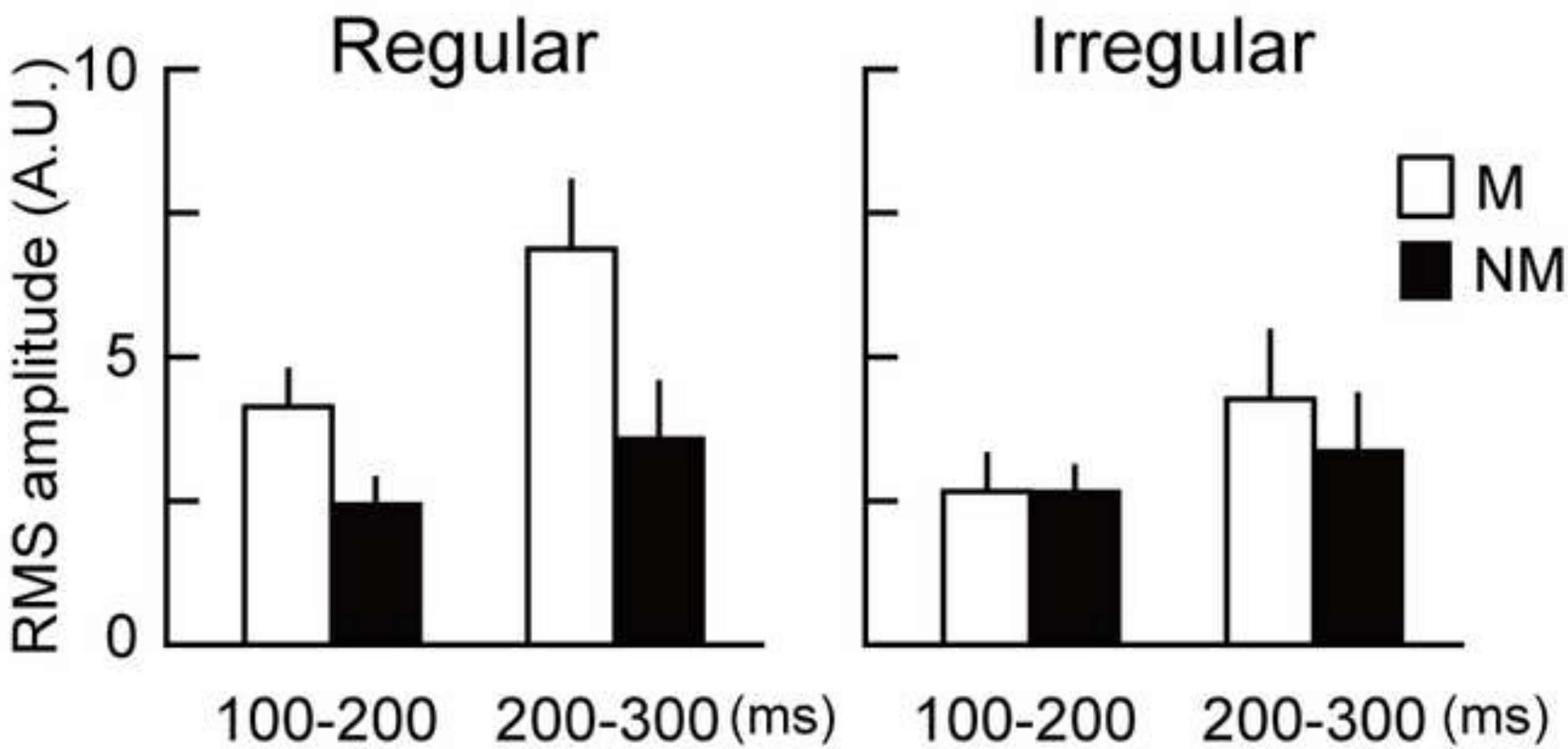

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Table 1

Peak coordinates of significantly activated areas for each 100-ms time window in the three-way ANOVA with factors musical experience, regularity, and position of the omission (uncorrected $p < 0.001$).

Brain area (Brodmann's Area [BA])	Peak coordinates *(x, y, z)*			Number of voxels	*z* value
100-200 ms					
Main effect of regularity (Regular > Irregular)					
Left Heschl's gyrus [BA41]	-51	-16	13	426	3.87
Right postcentral gyrus [BA43]	48	-12	18	57	3.30
Interaction of musical experience and regularity					
([Regular – Irregular] in musicians > [Regular - Irregular] in nonmusicians)					
Left Heschl's gyrus [BA41]	-51	-16	13	142	3.51
200-300 ms					
Main effect of regularity (Regular > Irregular)					
left superior temporal gyrus [BA22]	-53	-11	8	561	4.06
right superior temporal gyrus [BA22]	50	-12	9	328	3.66
Interaction of musical experience and regularity					

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([Regular – Irregular] in musicians > [Regular - Irregular] in nonmusicians)

left superior temporal gyrus [BA22]	-55	-7	6	209	3.43